

as such. Forssell (1883, 1884), basing his opinion upon the constant occurrence of cephalodia on definite species, also held this view, considering them adaptations for assimilation in that the blue-green and green algae together could absorb a wider range of the spectrum than one color alone. Elfving ('13, '31) attempted to prove that gonidia have a hyphal origin both in the lichen thallus and in the cephalodium but his conclusions have not been supported by recent work. That the theory of their parasitic nature is generally accepted can be seen by the fact that it was held by Th. Fries (1866), Schwendener (1869), Winter (1877), Babikof (1878), Moreau ('21, '28; M. and Mme., '15, '18, '32), Goebel ('26, '28), Tobler ('32), and Kaule ('32, '34).

The origin and development of the cephalodium have been described in *Peltigera (Peltidea) apthosa* (Babikof, 1878; M. and Mme. Moreau, '19; Darbishire, '27, '32), *Lobaria (Sticta) linita* (Winter, 1877), *L. (S.) oregana* (Schneider, 1897), *Solorina octospora* (Winter, 1877), *Lobaria (Ricasolia) herbaceae* and *L. (R.) amplissima* (Moreau, '21). Forssell (1883, 1884) and Kaule ('32, '34) have made anatomical studies of the cephalodia in a large number of genera and species.

The taxonomic value of the cephalodium was first suggested by Nylander (1860), who distinguished three types of gonidia in the structure: (1) stratum gonimon scytonemoideum, (2) stratum gonimon sirosiphonoideum, and (3) stratum gonimon e modulis gonimicis formatum; and adopted these different types as the distinguishing characteristics of different species. Since that time the type of gonidium has been used to differentiate species in the genus *Stereocaulon*, even though Th. Fries (1866) found all three in the same cephalodium. Riddle ('10) gave statistical data to support his opinion that the kind of alga is a good distinguishing character between certain species. Magnusson ('26) stated that the cephalodia have great taxonomic value, suggested that the species with *Nostoc*-algae are more closely related to each other than to species with *Scytonema*-algae, and recommended the investigation of these structures from various points of view. Frey ('33) neglected such characters in his treatment of the genus, and stated

that until pure culture methods demonstrate whether or not the choice of cephalodial gonidia is specifically parallel with that of normal gonidia we must be content with gross morphology in our bounding of species. A critical survey of cephalodia, based upon species of *Stereocaulon*, has not previously been made.

MATERIALS AND METHODS

The herbarium of the Missouri Botanical Garden and the private herbarium of Dr. C. W. Dodge, supplemented by minor collections from other sources, furnished ample material for the study of species of *Stereocaulon* from most regions. The value of the cephalodia in taxonomy and phylogeny may be observed: (1) by the correlation of their gross and microscopic morphology with other structures of the lichen; and (2) by a comparative study of their origin and development. Accordingly, free-hand sections were made of the cephalodia and of other parts of the various species, and an attempt was made to correlate the different characters of these structures. In addition, complete developmental series of each type of cephalodium were embedded in paraffin, sectioned at 10 μ , stained in Heidenhain's iron-alum haematoxylin, and mounted in balsam. Slides prepared in these ways were considered sufficient to test possible hypotheses.

Th. Fries (1857, 1858, 1866) had recognized two general types of cephalodia in this genus: one typified by these structures as they appear in *Stereocaulon paschale* and *S. denudatum*, the other as they appear in *S. ramulosum*. In addition to these two groups, Dodge ('29) recognized a third major division in his key, typified by the appearance of these bodies in *S. botryophorum*. These divisions, based upon the gross morphology of the cephalodium, seem to be comparatively stable and have been accepted as natural units in this paper. Then the present paper is really an attempt to formulate in some measure the extent to which the above groups express natural relationships.

The practical taxonomic value of a structure is its constant occurrence. Of three hundred specimens of *Stereocaulon*

taken at random from the herbarium, 87 per cent possessed an abundance of cephalodia, whereas only 68 per cent were fertile. Thus cephalodial characters, compared to apothecial characters, are more valuable if this fact alone is considered. If the validity of these clues to the identity of the 32 per cent sterile material can be tested, this study will be of practical value, for the correct determination of such material will undoubtedly enrich the distribution records of many species.

CRITERIA FOR PHYLOGENETIC SEQUENCE IN STEREOCAULON

In a study of phylogenetic relationships it is necessary to have some idea as to what characters are primitive and what are advanced within this genus. To evaluate these criteria it seems best to formulate the general trend of evolution within the family Cladoniaceae. This family differs so markedly in thalline development from other members of the Cyclocarpineae, i. e., in that it possesses a primary thallus from which a podetium or secondary thallus develops, that it is generally considered to be monophyletic in origin (Smith, '21). The primary thallus may be crustose, squamulose, or foliose, and the secondary thallus which arises from it is always fruticose. The podetium is terminated by apothecia and may be simple or branched. The spores are hyaline and range from one to many-celled. Cephalodia may or may not be present. The apothecium in this family is biatorine or lecideine, the most characteristic difference from other families being in the degree of development of the thallus described above. Glancing at the characters enumerated one can easily see that the phylogenetic starting point of the Cladoniaceae is undoubtedly to be found in a simple lichen possessing a crustose thallus, hyaline, one-celled spores, and a biatorine or lecideine apothecium. The apothecial stalk, by elongation (Reinke, 1894-1896; Wainio, 1897), secured good light conditions for the fruit and facilitated the distribution of spores (Smith, '21), resulting in a lichen bearing a single terminal apothecium on a stalk, similar to *Baeomyces*. Later the podetium increased in size and branching due to the assumption of vegetative functions;

in the genera in which vegetative development of the secondary thallus was very great the primary thallus tended to disappear. In some genera in which the podetial development is not so pronounced the common evolutionary trend from crustose to foliose primary thallus can be traced.

The genera of the Cladoniaceae might be arranged in a scheme such as is shown in fig. 1. In the left-hand branch one can trace the advance from a crustose to a foliose primary thallus (though it often disappears in some species of *Cladonia*), an increase in spore septation from *Gymnoderma* to *Heteromyces*, but remaining one-celled in the branch leading to *Cladonia*. The center branch has advanced primarily in spore septation. Some species of *Baeomyces* have septate spores; *Thysanothecium* has 1-2-celled spores, *Glossodium* 2-4, and one species of *Gomphillus* 100. At the top of this series, the primary thallus, although retaining its crustose form, has degenerated to a homoiomerous condition. The right-hand branch differs from the other two in the possession of cephalodia, usually occurring on the primary thallus of *Pilophoron* (which is primitive in having one-celled spores and a podetium that is seldom branched) and on the secondary thallus of *Argopsis* and *Stereocaulon*. In this branch an increase in the septation of the spores can also be traced (*Argopsis* forming a side branch with muriform spores). Degeneration of the primary thallus is likewise evident, for in most species of *Stereocaulon* and in *Argopsis* this structure is evanescent.

From a glance at this scheme of evolution within the Cladoniaceae it is fairly evident that the following may be considered as trends to advancement in relation to *Stereocaulon*: (1) increase in the septation and consequently in the length of the spore, (2) development of a large, branching, fruticose podetium, (3) degeneration of the primary thallus, and (4) development of cephalodia. To prove the taxonomic value of cephalodia it is now necessary to show that cephalodial characters are correlated with the tendencies noted above as well as with other characters useful in the determination of species of this genus.

To what extent may the presence of cephalodia be considered a derived character? If cephalodia are due to the presence of parasitic algae, as is ordinarily assumed, they can hardly be so considered—although the extent of adaptation against the disease could easily be—but if it is believed that

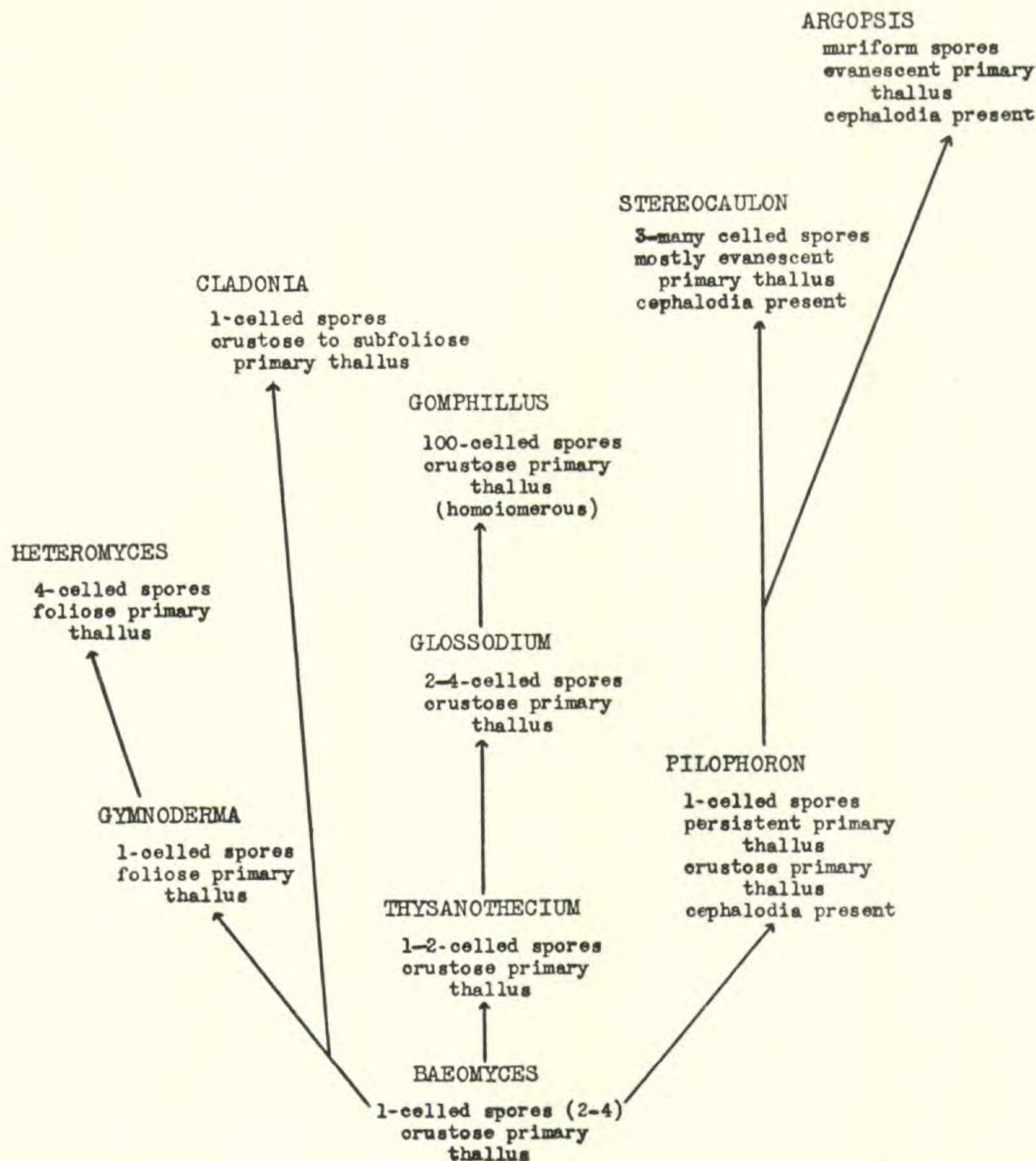


Fig. 1. A diagrammatical presentation of the phylogenetic connections within the family Cladoniaceae suggested in the text.

the blue-green algae are also in symbiotic relationship with the fungal constituent of the lichen, considerable phylogenetic significance must be associated with their presence.

Lichens are polyphyletic in regard to fungal and algal components, and it is commonly assumed that when similar algae

are held by different fungi they are of independent origin, whereas when different algae are held by the same fungus they are of common origin. Yet although the same fungus apparently may utilize various algae, the presence of two algae in the same thallus is rather rare, being common only in the few species producing cephalodia and perhaps in certain species of *Solorina* (the latter case depending upon whether or not the blue-green algal mass in such species as *S. crocea* is considered a cephalodium; see Hue, '11). Thus several systems (Reinke, 1894, 1895, 1896; Zahlbruckner, '26; Smith, '21) recognize chlorophyll and cyanophil groups as being relatively distinct.

In considering antiquity of symbionts it is believed that lichens containing green algae are the older group whereas the cyanophils are of relatively recent origin (Forssell, 1885; Hue, '11; Smith, '21). From the standpoint of theory it is reasonable to assume that the fungus of the lichen, first adapted to symbiosis with green algae, later adapted itself to an additional symbiotic union with blue-green algae. Although it is improbable that all lichens with cephalodia are closely related, the tendency to form these structures usually persists through an entire family or tribe and these families or tribes are usually recognized as being relatively high in their respective series.

Cephalodia have not yet been reported in the Pyrenocarpeae and Graphidineae. In the Coniocarpineae they occur only in *Sphaerophorus*, the terminal genus of that group. The cephalodia-bearing plants of the Cyclocarpineae belong for the greater part to the Stictaceae, Peltigeraceae, and Pannariaceae (the three most highly developed families of the Phycolichens) and to the *Pilophoron*, *Stereocaulon*, and *Argopsis* branch of the Cladoniaceae (a family which terminates an evolutionary branch in the Archilichens). It seems significant that all genera of foliose and fruticose lichens producing cephalodia are commonly recognized as advanced. There are, however, some relatively primitive crustose genera, e. g., *Lecidea* and *Lecanora*, which contain a few cephalodia-bearing species. The antiquity of these crustose genera and the large number of species within the genera would make it quite possible for a

few species to adapt themselves to the production of cephalodia (see Kaule, '32). The reason for this occurrence primarily in advanced groups, thus indicating an advanced character, is not understood. The real physiological significance of the cephalodium is not known, and few theories to account for its presence have been advanced. The prevalent opinion is that such structures are pathological growths which injure the host plant (see page 731). This does not seem to be the logical explanation, however, at least as far as their occurrence in the genus *Stereocaulon* is concerned. The question will be considered in greater detail later. It has been suggested, and it is indeed likely, that these bodies aid in nitrogen fixation (Cengia Sambo, '23, '26, '31; Darbishire, '24, '27). If this be true the degree of advancement can readily be appreciated, the fungus being specialized to the extent that it can utilize one alga to manufacture its usual food and an alga of an entirely different nature for its nitrogenous material.

From the evidence so far adduced one might be justified theoretically in holding that the species of *Stereocaulon* without cephalodia are more primitive than those that possess them. Yet one should not depend upon one structure for the state of advancement that a group of individuals may have attained, and particularly so when that character is a vegetative one. Since an acceptable system is always based upon a combination of characters, we may here consider the association of the types of cephalodia and the absence of cephalodia with other vegetative and with sexual characters.

TYPES OF CEPHALODIA

Nylander (1876), Forssell (1883, 1884), and Schneider (1897) have classified cephalodia into several subdivisions. The cephalodia of *Stereocaulon* fall into the epigena group of Forssell's *cephalodia vera*, into Nylander's *cephalodia epigena*, and into Schneider's ectotrophic group. The cephalodia of this genus have a varied gross morphology, and on this basis may be divided into three groups as suggested by Dodge ('29). Merely for the sake of convenience, these may be desig-

nated as spherical, botryose, and scrobiculate, characterized as follows:

Spherical: Cephalodia sessile or nearly so, at times partly immersed, often inconspicuous, hemispherical to subspherical, small, seldom over 1 mm. in diameter, the larger ones appearing in aggregates or irregularly rounded, gray to brown masses (pl. 66, figs. 1 and 2).

Botryose: Cephalodia often stalked at maturity, similar in shape to bunches of grapes, concolorous with the podetium, cinereous to glaucescent, usually rather large, 2–4 mm. in diameter (pl. 66, figs. 3 and 4).

Scrobiculate: Cephalodia usually stalked at maturity, globular but more or less clavate, pitted and furrowed with fine convolutions, concolorous with the podetium, whitish to ashy, often large and numerous, 1–7 mm. in diameter (pl. 66, figs. 5 and 6).

These groups are apparently very distinct. In mature material with an abundance of cephalodia it is almost impossible to make a mistake in determining the relationship. In exceptionally young material, however, both the botryose and scrobiculate cephalodia appear as small spherical bodies, and occasionally there is a conglomeration of spherical cephalodia (usually formed by the growing together of several whose origin was near a common point) which sometimes approaches the botryose condition, although never completely so. Few of these exceptional cases occur, and if there are enough cephalodia on the material examined (as is normally the case) so that the range of variation can be easily seen, the groups as a whole are very uniform.

THE ORIGIN AND DEVELOPMENT OF CEPHALODIA

Young podetia of *Stereocaulon* possess a cortex and an algal layer in addition to the central cylinder. In mature specimens, however, a cortex is present only around the phyllocladia and cephalodia (Schwendener, 1860; M. and Mme. Moreau, '32) which occur in scattered spots. Evidently these layers have burst due to growth of the central cylinder, and algae other

than those in the two organs mentioned above lie in small groups here and there in a loose tissue around the axis of the lichen (Kaule, '32). The cephalodia arise on this relatively naked, secondary axis—which in longitudinal section shows two fairly well-defined layers: an inner axis composed of usually parallel, thin hyphae, and an outer layer of thicker, more gelatinous hyphae, often interwoven. Certain blue-green algae fall on this outer layer and initiate cephalodia.

The account below is based primarily upon complete developmental series of cephalodia of the following species:

Spherical group: *Stereocaulon paschale* and *S. tomentosum*.

Botryose group: *Stereocaulon exutum* and *S. japonicum*.

Scrobiculate group: *Stereocaulon ramulosum* and *S. ne-saeum*.

Less extensive series were available in the nature of free-hand sections of the cephalodia of several other species.

Spherical: The blue-green algal clusters on the podetium vary from microscopic to rather large-sized (a colony of *Nostoc* 4 mm. in diameter was found on a moistened specimen of *S. tomentosum*). The presence of certain of these algae starts cephalodial development; the hyphae of the outer layer of the podetium elongate considerably and surround the algal cells (pl. 67, fig. 1). Hyphal branches grow into the interior from all sides of the enclosing wall thus formed and penetrate between the cells or filaments of the alga (pl. 67, fig. 2). Usually penetration has taken place to the extent that the normal appearance of the host alga is obliterated and it is now seen as small single-celled units embedded in a spherical mass of interwoven hyphae (pl. 67, figs. 2 and 3). The algae begin to divide and secrete a gelatinous sheath which is closely surrounded and sometimes penetrated by the fungus (pl. 67, fig. 5). The wall of the cephalodium and the outer layer of the podetium dissolve at the point of contact and the hyphae surrounding the blue-green algae are thus brought in closer relationship with the interior of the lichen. By further growth these hyphae become interwoven with those of the central cylinder of the

podetium, often anastomosing and fusing with them. This connection with the podetial axis is very distinct but a long stipe is not formed by cephalodia of this group. In younger stages the close adherence of the fungal hyphae to the gelatinous sheath surrounding the algae gives the appearance of a number of "capsules" in the interior of the cephalodium in which the algae lie (pl. 67, fig. 5). This stage persists for a short time only; probably the sheath becomes less viscous in mature cephalodia, for it then appears more diffuse and the fungal elements form hyphal plates so that a chamber-like division into several portions results (pl. 67, figs. 4, 6, and 7). The algae are kept in intimate contact with the central cylinder of the podetium at all times by hyphae running from chamber to chamber and finally to the central axis of the lichen. In the earlier stages the algae of the cephalodia would usually be identified as *Gloeocapsa*, but by the time the chambers have differentiated the colonies have assumed their typical form in cephalodia with *Stigonema*, *Scytonema*, or *Nostoc*. The hyphal plates are of varying thicknesses, and near their point of origin, i. e., near the wall of the cephalodium, often pass into a sort of pseudoparenchymatous zone. Farther toward the outside is the wall, composed of thicker, peripheral hyphae (pl. 67, figs. 5, 6, 7, and 8). The wall is comparatively thin and never is as distinct as in the scrobiculate type (e. g. in *S. ramulosum*, pl. 68, fig. 8). A conspicuous stalk is only rarely formed, although occasionally the hyphae running from the clumps of algae to the central cylinder of the podetium are quite well developed and so resemble one. The shape of the cephalodium is primarily dependent upon that of the algal mass about which it was built. If the mass were small the cephalodium would tend to be spherical or subspherical, but if it were extended, flattened, or linear that shape could also be assumed.

After the cephalodium has spent some time in vegetative growth a deterioration of its algae can be observed. This is first noted merely as a loss of color but later is clearly evident as an alteration in the structure of the algal cells. The cell content shrinks, and cavities can be seen within the gelatinous

sheath. Later the sheath itself becomes wrinkled and lobed abnormally. Even in young stages a large number of dead cells are found; in older stages only empty membranes are visible. The algae often are totally absorbed by the lichen, and with the death of the algae the walls of the hyphae in the cephalodium thicken noticeably. These hyphae seem to be without further function.

Summarizing we can say that the cephalodia of this group are relatively primitive because they have indefinite shape and a loosely arranged wall, and because they are sessile, rarely producing a well-defined stipe.

Botryose: The cephalodial primordium of the botryose group is very similar to that of the spherical group. A single cell, a small filament or a colony of blue-green algae coming in contact with the podetium is immediately surrounded by hyphae from the outer layer. The algal cells then come to lie more or less at random in a spherical mass, the hyphae merely being interwoven (pl. 67, fig. 9). Hyphal branches grow from this surrounding wall, and no matter what alga may be present at this stage its cells are independent units separated by the fungus (pl. 67, fig. 10). The algae continue to divide, and a gelatinous sheath is formed around the *Gloeocapsa* colonies or the *Nostoc* and *Stigonema* filaments (pl. 67, figs. 11 and 12). As in *Stereocaulon paschale* and *S. tomentosum*, this sheath is closely surrounded by the hyphae of the fungal component. At this time the outer layer of the podetium and the wall of the cephalodium coalesce; the hyphae of the inner part of the cephalodium grow through and become attached to the central cylinder of the podetium. Thus an intimate union is formed between the capsulated algal groups and the central cylinder of the lichen at an early stage. The wall of the cephalodium differs markedly from that of the scrobiculate type in that it is looser, much thinner, and is composed of interwoven rather than of periclinal hyphae (pl. 67, fig. 14). This interwoven wall sometimes appears to be intermediate between the peripheral orientation of the hyphae common in the spherical group and the periclinal orientation in the scrobiculate type. The

walls of the cephalodia of the two former groups are undoubtedly less highly specialized than those of the latter. As in the case previously described, the gelatinous sheath of the algae becomes less evident with age and diffuses out. The surrounding hyphae then form hyphal plates which divide the cephalodium and its algal content by several partitions (pl. 67, fig. 13). The method of lobe formation appears to vary slightly. In some young cephalodia the algae come to lie near the outer wall. In this case neither complete lobes nor complete hyphal plates are formed, but the cephalodium rounds out conforming to the spatial limitations imposed by the partially formed plates. Thus, although the lobes are rather distinct they are not chambered units in the cephalodium. The algal layer follows, in general, the contour of the lobes near the outer wall. The other type of lobing is apparently the normal one. The hyphal plates surrounding the algal colonies, as described above, grow so as to enclose them almost completely before making their connection with the central cylinder of the podetium. Growth and division of the algae inside the chambers thus formed expand them into the lobes so visible externally (pl. 67, fig. 15). The number and size of lobes formed are not definite, and there is no variation in the gross morphology of the two types of botryose cephalodia described. The arrangement of the algae in the cephalodium is quite varied but often seems to be correlated with the source of light. In old cephalodia the stages previously recorded in the deterioration of the algae are very numerous.

From the standpoint of anatomical structure this type of cephalodium is seen to have advanced from the condition found in the spherical group in that it has acquired a more definite form, a more highly developed conducting system, a wall often composed of interwoven rather than of peripheral hyphae, and usually a well-defined stipe.

Scrobiculate: A cell, filament, or colony of *Gloeocapsa*, *Nostoc*, *Stigonema*, *Scytonema*, and possibly related genera, may initiate the cephalodium in this group (pl. 68, fig. 1). Most of these have been found within a single cephalodium of a plant.

The type of alga does not alter the gross morphology of the structure; and the microscopic structure is only slightly different with different algae. The primordium is surrounded by hyphae which arise from the outer layer of the podetium and form a spherical mass, similar to the same stage in both the spherical and botryose groups (pl. 68, fig. 3). Hyphal branches grow inward from this enclosing layer and penetrate between the cells of the alga. By this time the alga has usually divided a few times, and if a filamentous or colonial form were present it has now been separated so that its cells appear as individual organisms (pl. 68, fig. 2). The algal genus cannot be distinguished at this stage. These cells lie apparently at random in a dense spherical mass of hyphae. The mass is uniformly dense and no outer wall has been formed.

The algae continue to divide and each cell that is now separate seems to give rise either to a small colony or a filament which becomes surrounded by a gelified sheath. The hyphae of the fungus form a firm layer closely adnate to each sheath (pl. 68, figs. 6 and 10) from which hyphal connections can be traced back into the central cylinder of the podetium in median sections (pl. 68, figs. 5 and 7). After this, the hyphae divide the algae into several masses, forming plates around the various clusters. Simultaneously, several hollow spaces are formed (especially noticeable in cephalodia containing *Nostoc* or *Gloeocapsa*) through which interlacing hyphae run from clump to clump and then into the podetium (pl. 68, fig. 4). The wall of the cephalodium has been forming during this time, and is now about one-half of its probable thickness at maturity, consisting of thick, more or less periclinal hyphae but interwoven enough to produce a firm, unbroken wall. Long search has not revealed an opening in the outer wall of the cephalodium. The entire structure is still spherical or ovoid.

Later convolutions form and the structure becomes more or less pitted (pl. 66, figs. 5 and 6). This is apparently due to the looseness of the conducting hyphae and the arrangement of the algal masses in a favorable position with reference to the source of light. At this stage a visible stalk is usually

formed, rudiments of which can be seen microscopically in very early stages. The stalk consists of two layers: the cephalodial wall, and the core of conducting hyphae. The core sometimes extends as much as one-third of the diameter into the cephalodium and may or may not form before lobing takes place (pl. 68, figs. 4 and 5). In median longitudinal sections its primordia may be seen at the time that the definite gelatinous sheath is first formed. The cephalodial wall has increased in thickness, presumably simply by elongation of the periclinal hyphae (pl. 68, figs. 8 and 11). It is composed of a closely packed tissue of hyphae and thus is quite different from the wall of the podetium which is of comparatively loosely interwoven hyphae. The mature cephalodium consists of this compact wall with the outline of a stalked, irregular pocket filled with a tissue of loosely interwoven filaments and hyphal plates intimately associated with blue-green algal masses (pl. 68, fig. 11). In cephalodia with *Nostoc* and *Gloeocapsa* the algae seem to be scattered in groups, but in those with *Stigonema* and *Scytonema* they occupy almost the entire cavity. The destruction of the algae (pl. 68, figs. 9, 12, and 13), previously mentioned in old cephalodia, with a corresponding thickening of the cephalodial hyphae after their death, is very evident.

Several times young cephalodia forming on the wall of fully developed cephalodia are found (pl. 68, fig. 2). The mode of origin and subsequent development are the same as though they had occurred on the podetium. In very young stages connecting hyphae are sent through the wall of the older cephalodium and make contact with its conducting hyphae; at the point of contact the cephalodial wall is destroyed. This observation easily explains how two kinds of algae might be found in the same cephalodium.

Anatomically considered, the scrobiculate group contains the most advanced cephalodial type. The specialized shape of the cephalodium, the highly developed conducting system, and well-defined stipe, together with a derived wall structure, raise it far above the other groups, for none of them possess all of these characters.

CHARACTERS ASSOCIATED WITH THE TYPES OF CEPHALODIA

The genus *Stereocaulon* has great variability in the characteristics of its members, somewhat similar to that found in the closely related genus *Cladonia*. Thus specific relationships must be settled upon combinations of characters, and these characters often vary considerably within a species. Spore sizes have minor variations among species in most groupings of this genus but on the whole are so uniform as to be without value in specific diagnosis (Riddle, '10). In general, spore characters are the most conservative (note emphasis of Watson, '29, and Gilbert, '27, on them), and since the elongation and increasing septation of the spores cannot be shown between species they would be expected to show within the family (see p. 734). From table 1 it is indeed quite apparent that there is a gradual elongation of the spores and an increasing septation of the same structures within the groups based on cephalodia, in the following order:

Cephalodia lacking: The apothecia also are often lacking. Only one species, *Stereocaulon pygmaeum* (specimens not seen by the author), which, according to Dodge ('29), belongs in this section, has been reported with spores. Dodge gives the spores of this species as 13–15 μ in length, 3-septate.

Spherical: spores 20–39 μ in length, 3–7-septate.

Botryose: spores 24–100 μ in length, 3–16-septate.

Scrobiculate: spores 35–200 μ in length, 3–29-septate.

It is also seen, as would be expected, that other associated fruiting characters (often used in distinguishing species in this genus), such as length of asci, height of hymenium, and thickness of hypothecium, are correlated with the length and septation of the spores. Furthermore, it is significant that the evidence obtained from this comparison agrees in every detail with that derived from anatomical studies of the origin and development of cephalodia in that the groups may be arranged as follows, each one in sequence indicating a more advanced condition: spherical, botryose, scrobiculate.

Advanced species of *Stereocaulon* have been predicted to

TABLE I
CORRELATION OF CERTAIN APOTHECIAL CHARACTERS WITH THE
CEPHALODIAL TYPES¹

Cephalodia	Species	Spore length in μ	Spore septa	Thickness of hypothecium in μ	Height of hymenium in μ	Length of ascus in μ
Lacking	<i>albicans</i> <i>arbuscula</i> <i>congestum</i> <i>gracilescens</i> <i>nanum</i>	Apothecium lacking				
Spherical	<i>condensatum</i>	25-35	3	30-50	40-50	35-45
	<i>pileatum</i>	20-30	3	20-30	50-60	43-55
	<i>alpinum</i>	25-35	3	35-40	45-60	35-50
	<i>coralloides</i>	20-35	3-5	35-50	50-60	40-45
	<i>cornutum</i>	28-32	3	40-65	46-60	42-50
	<i>denudatum</i>	22-38	3-5	25-35	50-70	40-50
	<i>glareosum</i>	25-37	3	25-40	45-55	48-50
	<i>nabewaziense</i>	30-35	3-4	45-60	45-60	35-52
	<i>paschale</i>	28-39	3	45-60	50-65	35-50
	<i>rivulorum</i>	30-35	3	35-50	60-70	55-60
	<i>sphaerophoroides</i>	35-38	3	45-60	45-60	43-50
	<i>tomentosum</i>	25-35	3-7	45-60	45-60	35-45
	<i>Wrightii</i>	Apothecia not seen				
Botryose	<i>botryophorum</i> ^{*2}	75	11	-	-	-
	<i>corticatum</i>	25-40	3	60-80	60-95	50-75
	<i>curtatum</i>	36-40	3-7	55-70	70-95	65-85
	<i>exutum</i>	30-48	3-5	80-88	80-105	70-85
	<i>foliolosum</i>	94-100	14-16	74-95	120-140	105-120
	<i>japonicum</i>	25-48	3-5	45-75	72-96	50-85
	<i>nigrum</i>	40-50	3-7	45-80	70-95	60-75
	<i>octomerellum</i>	34-55	3-7	60-85	75-98	70-85
	<i>prostratum</i>	24-30	3	65-75	80-105	50-78
	<i>uvuliferum</i>	25-35	3	65-75	65-82	52-70
Scrobiculate	<i>chlorocarpoides</i>	75-100	5-9	65-80	135-190	110-160
	<i>lecanoreum</i> [*]	72-80	5-7	-	-	-
	<i>macrocarpum</i>	40-70	3-5	95-110	105-140	70-90
	<i>macrocephalum</i> [*]	200	19-29	-	-	-
	<i>mixtum</i>	36-75	3-5	50-90	65-110	60-90
	<i>nesaeum</i>	70-120	5-12	70-90	120-150	105-135
	<i>pilophoroides</i>	50-65	5-9	80-110	95-140	80-110
	<i>piluliferum</i>	60-110	5-15	80-105	120-200	90-160
	<i>proximum</i>	40-70	3-5	45-85	75-110	60-90
	<i>ramulosum</i>	35-95	3-5	50-94	70-120	50-110
	<i>sinense</i> [*]	132-155	29	-	180-200	176-190
	<i>sorediiferum</i> [*]	100-110	7-9	-	150	88-115
<i>strictum</i>	80-90	3-7	65-85	130-170	105-120	

¹ Values recorded in tables I and II do not apply to type or authentic material in all cases, but represent the range of the available herbarium material determined to the species listed. Since in many cases only a few specimens were present it might be expected that the average and even extreme figures would differ slightly had additional material been available.

² Specimens of species marked with an asterisk were not seen. Figures cited here are taken from the original type descriptions or from subsequent examination of the types and are included to give a more complete conception of the extremes of certain groups.

have evanescent primary thalli. This is true of all the species considered with botryose and scrobiculate cephalodia, which on the basis of certain apothecial characters, notably spore size and septation, have been indicated as being most advanced. Two species in the section with spherical cephalodia, i. e., *Stereocaulon condensatum* and *S. pileatum*, have persistent primary thalli. The presence of spherical cephalodia, a small podetium, short, few-septate spores, and a persistent primary thallus have all been indicated as being primitive characters. Thus it seems that the two species mentioned fulfill all of the requirements of a primitive state, and on that basis must be designated as the group that is in all probability most similar to the ancestors of the representatives of *Stereocaulon* existing to-day. That group of species lacking cephalodia may have either a persistent or evanescent primary thallus, indicating a primitive condition, as does the absence of cephalodia itself (since these are derived characters). Perhaps this section could be considered even more primitive than the group with spherical cephalodia. Yet whenever such a state is indicated it is necessary to inquire whether the given combination of characters indicates a truly primitive or merely a reduced condition. Since the probable ancestors of *Stereocaulon*, forms similar to the genus *Pilophoron* (fig. 1), possessed cephalodia, at least on the primary thallus, it seems more logical to believe that the most primitive species of *Stereocaulon* should also have them. Thus the group under consideration can reasonably be assumed to have undergone a reduction from the primitive state designated above, the reduction being evident in the disappearance of cephalodia and often of apothecia, as well as in other correlated characters which will be mentioned below, tendencies logically connected with the arctic-alpine environment in which it occurs.

It was also considered that a small, erect, secondary thallus bearing a single terminal apothecium would represent a primitive condition, while a large, vigorously branching podetium bearing numerous apothecia would be more advanced. To a certain extent table II shows the variation predicted from family analysis, the extent of branching being indicated by the

number of main branches and the apothecial index (a term used to refer to the number of apothecia terminating the main branches and branchlets of the podetium—see note 4, table

TABLE II
CORRELATION OF CERTAIN VEGETATIVE CHARACTERS WITH THE
CEPHALODIAL TYPES¹

Cephalodia	Species	Size in cm.	Branching ³	Color	Apoth. index ⁴	Predominant type of phyllocladium
Lacking	<i>albicans</i>	.6-1.4	0-1	white		granular
	<i>arbuscula</i>	1-2	0-2	grayish		granular
	<i>congestum</i>	1.5-2	0-2	white		verruciform
	<i>gracilescens</i>	.5-1.5	0-1	white		granular
	<i>nanum</i>	.2-.6	0-3	whitish		granular
Spherical	<i>condensatum</i>	.3-1.2	0-1	gray-dark	0-2	granular-verruciform
	<i>pileatum</i>	.5-1.0	0-1	light-dark	0-1	granular to elongated
	<i>alpinum</i>	1-3	1-3	gray-dark	3-15	verruciform
	<i>coralloides</i>	2-4	3-5	white-gray	3-20	coralline
	<i>cornutum</i>	5-9	0-1	white-gray	0-2	coralline-flattened
	<i>denudatum</i>	1-7	0-3	gray-dark	0-6	flattened-umbilicate
	<i>glareosum</i>	1.5-2.5	2-4	grayish	3-8	cylindrical-terete
	<i>nabewaziense</i>	2.5-3	2-4	gray-dark	3-8	flattened-squamiform
	<i>paschale</i>	2-9	2-5	light-gray	0-14	palmate-digitate
	<i>rivulorum</i>	1-2	1-3	grayish	0-15	verruciform-umbilicate
	<i>sphaerophoroides</i>	3-5	2-7	gray	0-10	verruciform-elongate
	<i>tomentosum</i>	3-10	2-4	gray-dark	0-6	squamulose
<i>Wrightii</i>	3-5	0-2	grayish	-	absent	
Botryose	<i>botryophorum</i> ^{*2}	2-4	-	-	-	coralline
	<i>corticatulum</i>	.8-2.0	0-3	dark	4-8	granular-subcoralline
	<i>curtatum</i>	1-2	0-3	gray-dark	1-6	papilliform-coralline
	<i>exutum</i>	3-5.5	2-4	brown-dark	4-10	coralline
	<i>foliolosum</i>	2-4	3-4	light	0-3	coralline
	<i>japonicum</i>	1.2-3.5	0-4	dark	1-8	coralline-verruciform
	<i>nigrum</i>	2-4	0-4	dark-black	2-7	coralline
	<i>octomerellum</i>	.4-1.2	0-2	dark	1-3	coralline-subcoralline
	<i>prostratum</i>	.4-.9	0-1	dark-gray	1-2	subcoralline-coralline
	<i>uvuliferum</i>	2.5-5	1-4	gray-dark	2-10	coralline-terete

TABLE II—Continued

Cephalodia	Species	Size in cm.	Branching ³	Color	Apoth. index ⁴	Predominant type of phyllocladium
	<i>chlorocarpoides</i>	5-9	5-7	whitish	7-22	coralline-terete
	<i>lecanoreum</i> *	5-7.5	-	whitish	-	coralline
	<i>macrocarpum</i>	6-12	5-6	whitish	20-44	coralline
	<i>macrocephalum</i> *	1.5-4	-	-	-	coralline
	<i>mixtum</i>	4-8	6-10	whitish	17-48	coralline-terete
Scrobiculate	<i>nesaeum</i>	4-7	4-7	light	15-50	coralline-terete
	<i>pilophoroides</i>	6-12	3-7	whitish	15-52	coralline
	<i>piluliferum</i>	1.5-3.5	2-5	light	5-15	coralline-terete
	<i>proximum</i>	6-9	4-10	whitish	7-38	coralline-terete
	<i>ramulosum</i>	3-10	3-10	whitish	5-48	coralline-terete
	<i>sinense</i> *	2-4	-	-	-	coralline
	<i>sorediiferum</i> *	2-4	-	-	-	coralline
	<i>strictum</i>	4-7	4-6	light	4-11	coralline-terete

¹ See footnote 1, table I.² See footnote 2, table I.³ The values listed indicate the number of main branches of mature podetia.⁴ Apothecial index is the term used to refer to the number of apothecia terminating the branchlets of a podetium. It is a measure of the extent of main branching rather than of the fineness of the subdivisions or of the number of apothecia produced. The lateral apothecia of the species that produce them are not included here and in many cases (especially in species with spherical cephalodia) it is difficult to distinguish a sub-lateral from a terminal apothecium. The values then are more or less relative but do indicate the tendencies present.

ii). As can be seen, the section with scrobiculate cephalodia is by far the most advanced, having a size range of 1.5-12 cm. and an apothecial index of 5-52. The botryose and spherical (exclusive of the two species designated as primitive) groups occupy the reverse order expected, having a size range of 0.4-5.5 and 1-10 cm. respectively, and these are correlated with apothecial indices of 0-10 and 0-20. The number of apothecia produced on the podetium also agrees with these indications. The spherical group as limited here often shows almost as many fruiting bodies as the scrobiculate type, contrasted with the relatively few produced by the botryose section. That the latter section has the smaller podetium and less apothecia is perhaps due to the fact that the cephalodia, though undoubtedly more specialized, are fewer and that the apothecia are often unusually large. The differences, however, are great enough to indicate a more or less parallel development of the species with botryose and the advanced species with spherical

cephalodia rather than to harmonize with the hypothesis that one of these groups might have arisen from the other.

The nature of the phyllocladium is also considered of value in determining species. Each species has a typical form which, although quite variable and developing many different stages, gives a distinct appearance to the plant (Riddle, '10; Magnusson, '26). Tabulation of these organs (table II) for the various groups of cephalodia recognized shows that a particular type of phyllocladium is associated with a particular group. A reduced, granular structure is characteristic of the species without cephalodia; the species with spherical cephalodia show a transition from the granular to more highly developed (though quite varied) forms; and the botryose and scrobiculate groups usually possess well-developed, coralline phyllocladia that are often branched. Moreover, since the color and size also agree with the proposed grouping, the entire habit of the plant, considered important in distinguishing species of the genus, may be said to be correlated with the cephalodial types recognized in this paper.

The brown hypothecium, upon which the section *Phaeobasis* (Wainio, '15) was founded, appears sporadically among the divisions noted here. Although this character is at times used to distinguish species groups it evidently is not associated with any other character considered as having phylogenetic value. This same conclusion has already been reached by Redinger ('36) who points out such great divergencies between species of *Stereocaulon* with a dark hypothecium that on this basis alone they cannot be held closely related. Thus the section *Phaeobasis* should not be taken as an expression of natural relationship.

SPECIFICITY OF CEPHALODIAL GONIDIA

It is interesting to note that the cephalodial gonidia of *Stereocaulon* are always blue-green and not green algae like the normal gonidium. Also of possible significance is the fact that the ability to form such structures is generically defined. A dispute, however, has arisen as to whether there is any vari-

ability in the algae enclosed in these organs. Many Chlorophyceae and Myxophyceae occur as epiphytes on the podetium, especially of the tomentose species, whereas only a few genera have been identified in cephalodia. Nylander (1860) described several species of *Stereocaulon* based upon the nature of the cephalodial contents. Th. Fries (1866) found all of Nylander's types in a single cephalodium and consequently did not accept the latter's species, further postulating (although stating that he was not certain) that these types were three different stages in the development of a parasitic algal genus (*Stigonema* = *Sirosiphon*). Schwendener (1869) held that the algae did not change their appearance during development but stated that the three kinds of gonidia were three different algae (*Stigonema*, *Scytonema*, and *Nostoc*). Although Th. Fries found these types in a single cephalodium in 1866, leading lichen taxonomists have either neglected or refused to recognize his work, for they accepted species based solely on the kind of algae present (Nylander, 1888; Hue, 1898; Zahlbruckner, '27; Dodge, '29). Riddle ('10) and Magnusson ('26) have stated that the algal content of the cephalodium is a good specific character although Riddle recorded one specimen with two kinds of algae, while Magnusson found both *Nostoc* and *Stigonema* in the cephalodia of *Stereocaulon fastigiatum* and *S. paschale*. In *S. ramulosum* Schwendener (1869) and Forssell (1883, 1884) recorded *Nostoc* and *Stigonema*; Bornet (1873) reported *Scytonema* and *Lyngbya*. Frey ('33) found *Nostoc* and *Stigonema* in *Stereocaulon paschale*, *S. grande*, *S. denudatum*, and *S. botryosum*.

Certain facts obtained from the study of the development of the cephalodium should be emphasized here. In the early stages it is impossible to distinguish the genus of algae present. In some of these stages (especially in species of the spherical group) *Stigonema* and *Scytonema* (and sometimes *Nostoc*) contained in cephalodia would be identified as *Gloeocapsa*. Forssell (1883, note, p. 14) recorded transitions between *Gloeocapsa* and *Stigonema* in cephalodia. Furthermore, the form of the algal cells varies greatly, since continued division

causes them to become closely pressed together. Also (especially in species with scrobiculate cephalodia) filaments of *Stigonema* often appear like those of *Nostoc*, the division into the third plane being rather late in development. Mistakes in identification are easily made and especially so in free-hand sections mounted in glycerine or lactophenol and stained with such dyes as eosin, methyl blue, etc. For clarity in determination, embedding in a suitable medium and staining with iron-alum haematoxylin is recommended (the process used to make the counts recorded below). Since, as Th. Fries (1866) postulated, the algae undergo morphologic changes during the development of the cephalodium, they are at least a rather unstable taxonomic character.

Although it is true that changes during development take place, Schwendener's observation that various genera of algae occur in the cephalodium is equally true. Table III shows the results of the examination of a large number of cephalodia from several species, with an enumeration of the different genera of algae found.

Thus the genera of algae enclosed may vary considerably within a species, especially in the group with scrobiculate ceph-

TABLE III
VARIATION OF CEPHALODIAL GONIDIA IN CERTAIN SPECIES
OF STEREOCAULON

Type of cephalodia	Species	Collections examined	Cephalodia examined	Remarks ¹
Spherical	<i>alpinum</i>	10	250	3.6% S.; 96.4% N.
	<i>denudatum</i>	5	100	94% S.; 6% N.
	<i>paschale</i>	10	250	96.4% S.; 5.6% N. ²
	<i>tomentosum</i>	10	250	3.2% S.; 97.2% N.
Botryose	<i>exutum</i>	8	250	98.4% G.; 2.4% N.
	<i>japonicum</i>	5	50	100% G.
	<i>prostratum</i>	4	100	97% S.; 3% N.
Scrobiculate	<i>mixtum</i>	10	100	13% G.; 27% S.; 63% Sc.
	<i>nesaeum</i>	5	100	76% Sc.; 25% S.
	<i>proximum</i>	10	100	32% G.; 68% S.; 3% Sc.
	<i>ramulosum</i>	10	250	60.4% G.; 35.6% S.; 6.8% Sc.

¹ S = *Stigonema*, N = *Nostoc*, G = *Gloeocapsa* or *Chlorococcus*, Sc = *Scytonema*.

² When the sum of the percentages is greater than 100 per cent the presence of more than one algal genus in one or more cephalodia is indicated.

alodia. Perhaps one of the reasons for this is to be found in the fact that all the specimens examined with botryose cephalodia came from a limited area in Japan, those with spherical cephalodia came for the greater part from North America, whereas those of the scrobiculate group were collected in more scattered localities. Yet, whatever may be the limitations of the data, one point is unavoidable: i. e., that there is a variability in the algal content of the cephalodium, both in regard to the genera present and to the morphological appearance during development. For this reason it seems that species based on the nature of the cephalodial content alone cannot stand. Several species are evidently differentiated on the basis of this single character (e. g., *Stereocaulon ramulosum*, *S. mixtum*, and *S. proximum*; *S. nesaeum* and *S. Massartianum*). The data accumulated point to the fact that only the oldest name in each group of examples given above is valid and that the later segregates should not be accepted unless additional morphological characters are found upon which they can be based.

DISCUSSION

From the above considerations it seems logical to diagram the probable relationships within the genus *Stereocaulon* as shown in fig. 2. The primitive species apparently have short, few-septate spores, a persistent primary thallus, cephalodia on the primary thallus, few-branched podetia, granular phyllocladia, and minute, sessile cephalodia. From this group, possibly by subjection to severe environmental conditions that did not favor growth, the cephalodia (and often the apothecia) disappeared, and the phyllocladia often became greatly reduced. Some species of the primitive spherical group lost the primary thallus and became large and branching. With an increase both in spore size and septation, and a corresponding increase in correlated apothecial and vegetative characters, the line of evolution continued upward in three directions; one terminating in species with botryose, another in species with scrobiculate cephalodia, and the third containing the spherical ancestral type.

Although this study was to emphasize primarily the taxonomic and phylogenetic significance of these structures it is felt that some evidence has accumulated to assist in determining their true nature, about which little is known. Th. Fries (1866) gave no reason for his statement that the alga was

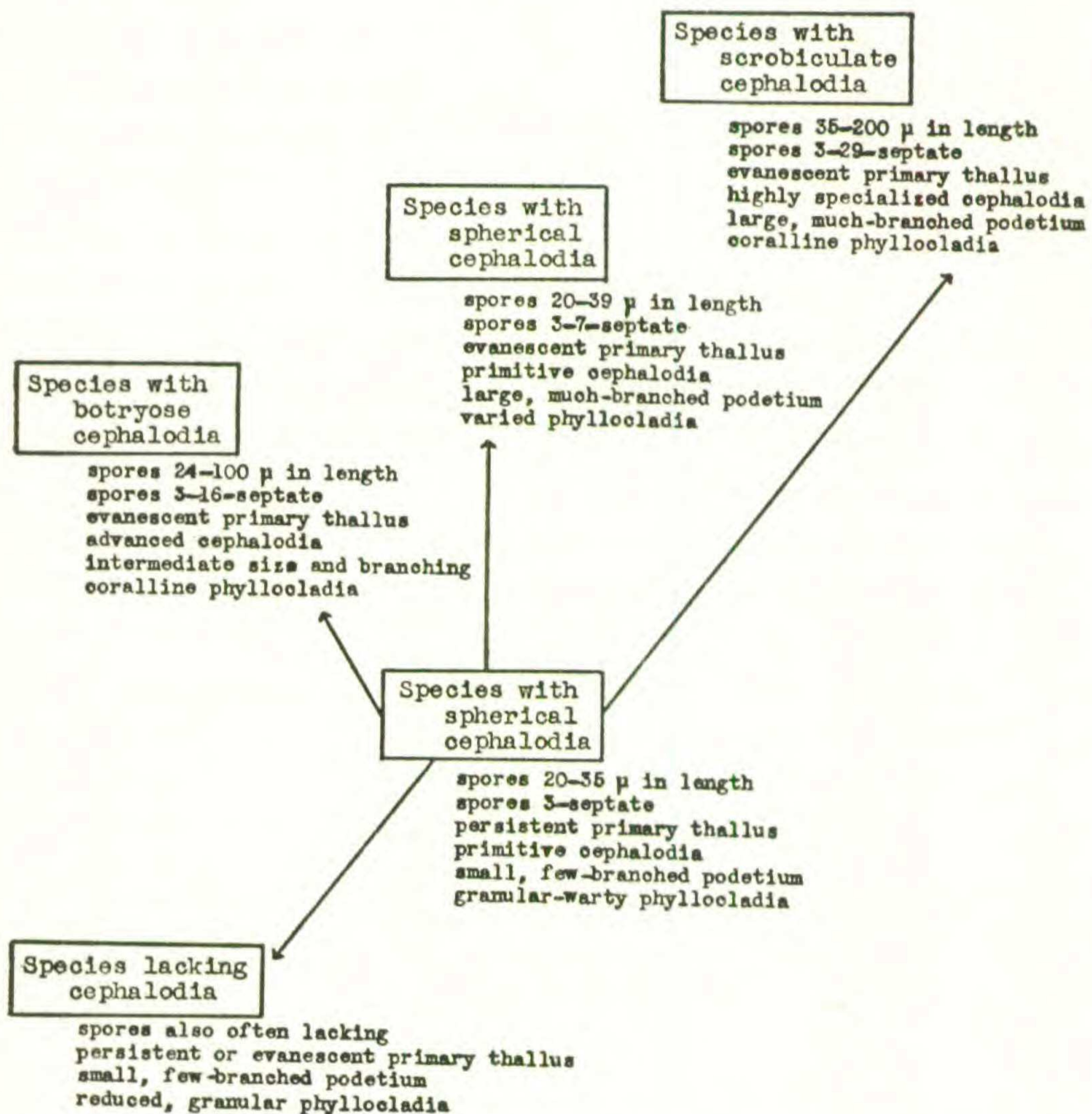


Fig. 2. A diagrammatical presentation of the phylogenetic connections within the genus *Stereocaulon* suggested in the text.

parasitic, nor did Schwendener (1869) who agreed with him. Winter (1877) designated cephalodia as parasitic structures, although he pointed out that the stimulus of the algae gives rise to unusual growth. Because of this increased growth one must conclude that the algae provide the hyphae with nourishment or cause them to hypertrophy through the effect of dis-

ease. Since the hyphae in no way appear diseased (although the algae often die) only the former opinion is tenable. The fact that there are fewer algal cells in young cephalodia and more in old ones proves that the algae, in spite of being surrounded by the hyphae, remain alive for some time and are capable of carrying on their life processes, even though they are visibly impaired by association with the fungus. Notwithstanding these facts, most writers regard cephalodia as pathologic structures! Reinke (1895) gave no evidence for considering them parasitic and left open the possibility that they are profitable to the lichen through power of assimilation. Winter (1877) and Babikof (1878) did describe some phenomena which were emphasized by Kaule ('32) to support his contention that cephalodia are harmful to the lichen. Goebel ('26) claimed to have seen hyphae penetrating from the cephalodium into the green algal layer and on into the thallus. Because of this anatomical appearance he considered cephalodia to be haustorial galls living parasitically on the lichen host. Darbishire ('27) could not find the haustorial hyphae Goebel mentioned. Kaule ('32) believed that he had proved the pathological nature of cephalodia, the evidence from an anatomical study of many groups seeming to point in that direction. This evidence is based largely upon the confirmation of Goebel's observation in a large number of genera and species, i. e., that hyphae from the cephalodium penetrate the lichen thallus into the green algal zone and bring about the destruction of the gonidial layer and its associated hyphae. In an additional report, Darbishire ('32) again stated that he could not find the haustorial hyphae referred to by Goebel ('26, '28) and Kaule ('32), and that he did not believe cephalodia to be haustorial structures. Kaule has also written a second paper ('34) upholding his previous statements.

So much has been written about the exact nature of the relation of the fungus to the alga in the lichen that it is hard to apply terms to the group as a whole. Schwendener, for instance, conceived of lichen symbiosis as the parasitism of a fungus on an alga, whereas M. and Mme. Moreau prefer to

think of the lichen as a disease of the fungus caused by the alga, in which the fungus is galled as insects gall phanerogams. Darbishire ('27) has noted the difficulty in showing that anatomically the fungus can be designated diseased by the alga, biologically as living peacefully with the alga for the good of the whole, and physiologically as active upon the alga. However that may be, this paper is not an attempt to decide the relationship of the alga to the fungus in the lichen body. The impression has been left by those who consider cephalodia parasitic bodies (Goebel, '26, '28; Kaule, '32, '34) that the cephalodium attacks the thallus (or podetium) in such a manner as to damage the organism. The writer cannot say whether or not this is true in all cephalodia-bearing groups; the opinion expressed here applies only in the case of *Stereocaulon*. It seems that in this genus cephalodia are beneficial to the organism rather than the injuring influences one might be led to believe. If of any benefit it must be vegetative in character (since only asexual elements are involved). Table II shows that specialized cephalodia occur on the podetia of the most vigorous species and there is usually a good correlation between the size of the lichen and the number of cephalodia on the plant. The most primitive species have poorly developed cephalodia, and since these organs have phylogenetic significance it seems reasonable to assume long, continuous, mutualistic relationship. None of the factors upon which Kaule ('32) based his belief that cephalodia in lichens are harmful have any foundation in *Stereocaulon*, since there is no continuous green algal gonidial zone in mature podetia. He even stated that no harm to the thallus by the cephalodium can be ascertained in this genus. This observation is here confirmed in every detail; neither macro- nor microscopic injury can be found. It may be possible to consider cephalodia pathological structures in other genera; indeed there is some evidence to support this view, but it is impossible to extend that concept to the genus treated here.

It does seem rather absurd, however, even in other genera, to imagine the hyphae of a perfectly healthy lichen forming a

union with an alga that grows more vigorously autotrophically than in the combined state, and to consider that the alga benefits and that the lichen is damaged because of such an association. The fungus is always the active component; the alga remains passive during the entire development. That the algae are capable of living outside of the lichen is testified by their healthy, normal appearance on the exterior of the podetium, in the tomentum, and on nearby soil. Babikof (1878) took them from cephalodia of *Peltigera aphthosa* and grew them for five weeks on sterile soil. Once inside the cephalodium, the alga, though apparently still in good condition, never retains the appearance it had in solitary life. Whether this is harmful to the blue-green algae might be debatable, but if the presence of dead algae is considered a good criterion (and Schwendener, 1867, 1869, and Bornet, 1873, have considered this the best support for the parasitic interpretation of lichen symbiosis), we can certainly consider that the fungus utilizes the algae of the cephalodium, for numerous algae are found dead there; moreover, they are often totally absorbed by the lichen.

Then there are several anatomical evidences in favor of the viewpoint upheld in this paper. (1) The definite wall structure such as is found in the scrobiculate type does not completely surround the algal mass, but only the outer part (pl. 68, fig. 5). When compared to insect galls, it should be noted that the insect is completely enclosed. Such is never the case in cephalodia of this genus; the algae are surrounded toward the outside and toward the inside are in actual contact with the lichen thallus, being in direct communication with the central cylinder of the podetium. (2) The fungal hyphae adhere closely to the algal components as though they were providing an absorption mechanism for the foodstuffs possibly produced at those points (pl. 67, figs. 5 and 12; pl. 68, figs. 6 and 10). (3) The conducting core leads to the central cylinder of the lichen, providing intimate connection with the cephalodium at all times (pl. 68, fig. 7). It seems hard to explain the presence of these structures unless they are used for the benefit of the fungus. Conclusive proof of the manner in which this bene-

ficial action takes place is not available, but Cengia Sambo ('23, '26, '31) and Darbishire ('24, '27) have suggested that cephalodia function in the fixation of nitrogen. This would explain the absence of cephalodia on some specimens; possibly they were growing on soil or rock where considerable nitrogenous matter was available. In 1926 (confirmed in '31) Cengia Sambo called attention to *Azotobacter* occurring in the gelatinous sheath surrounding the gonidia of the cephalodium. She postulated a symbiotic relationship between the bacterium, the fungus, and the algae. It is at least true that bacteria can often be seen in sections of cephalodia. At any rate, the action of cephalodia for the benefit of the lichen-fungus seems to be the most plausible hypothesis as far as species of *Stereocaulon* are concerned.

CORRELATION OF CEPHALODIAL TYPES WITH GEOGRAPHICAL DISTRIBUTION

Species with spherical cephalodia are distributed throughout the entire world as would be expected from their primitive condition, although they are more frequent in the northern hemisphere. The species of the north boreal zone are almost wholly of this type. That group which lacks cephalodia occurs intermittently but is to be found either in northern latitudes or in high altitudes, indicating perhaps the severe climatic conditions associated with the reduced nature of the species. Species with botryose cephalodia occupy a limited area in eastern Asia while those with scrobiculate cephalodia occur mainly in the tropics and in the southern hemisphere, though they rarely reach the southern extremity of the north temperate zone. Thus each advanced type of cephalodium occurs in a more or less restricted area. There is nothing in the actual geographical distribution to indicate that the grouping of the species of *Stereocaulon* as proposed in this paper is not a natural method.

SUMMARY

The cephalodia of *Stereocaulon* have been studied comparatively from the standpoint of their taxonomic and phylogenetic

value. The following conclusions seem justified with regard to this particular genus:

(1). That the gross morphology of the cephalodium is a good taxonomic character, and on this basis three types are recognized.

(2). That the presence of a cephalodium is an advanced character.

(3). That the cephalodia are not pathological structures, but seem to be beneficial to the entire lichen.

(4). That a small, sessile, spherical cephalodium is the primitive type. This is correlated with spore length and septation, the condition of the primary thallus, various apothecial characters (as length of asci, height of hymenium, and thickness of hypothecium), and in the habit or general appearance of the plant expected from a consideration of the evolutionary tendencies in the family to be primitive.

(5). That a certain group of species, having once acquired cephalodia, later lost them, the reduction being evident in the nature of the phyllocladia, in the general habit of the plant, and often in the loss of apothecia.

(6). That species with botryose and scrobiculate cephalodia represent well-stabilized advanced types, the cephalodial advances being correlated with the advances in other characters expected within the genus.

(7). That, on the basis of all data available, a phylogenetic scheme, such as is diagrammed on page 754, may be logically held to show evolutionary tendencies within the genus.

(8). That the type of alga in the cephalodium has no taxonomic, much less phylogenetic, significance, both because of the morphological variation during development and the variation in the genera of algae.

(9). That a study of the origin and development of cephalodia confirms the phylogenetic sequence presented; the primitive type of cephalodium being without definite wall, form, or stipe; the botryose type usually possessing a definite form and stipe, but a loosely developed wall; the scrobiculate type possessing a well-developed stipe, form, and wall. The origin and development of each of these types is described.

(10). That the geographical distribution of these groups is in agreement with the opinions expressed in this thesis.

The validity of the data presented in this paper can be determined only by the completion of a monograph of *Stereocaulon*. It is only in such a work that the most accurate placement of species according to their natural relationship can be made. At present more complete information must be obtained in regard to the cephalodial and other morphological characters of many, as yet poorly understood species.

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EXPLANATION OF PLATE

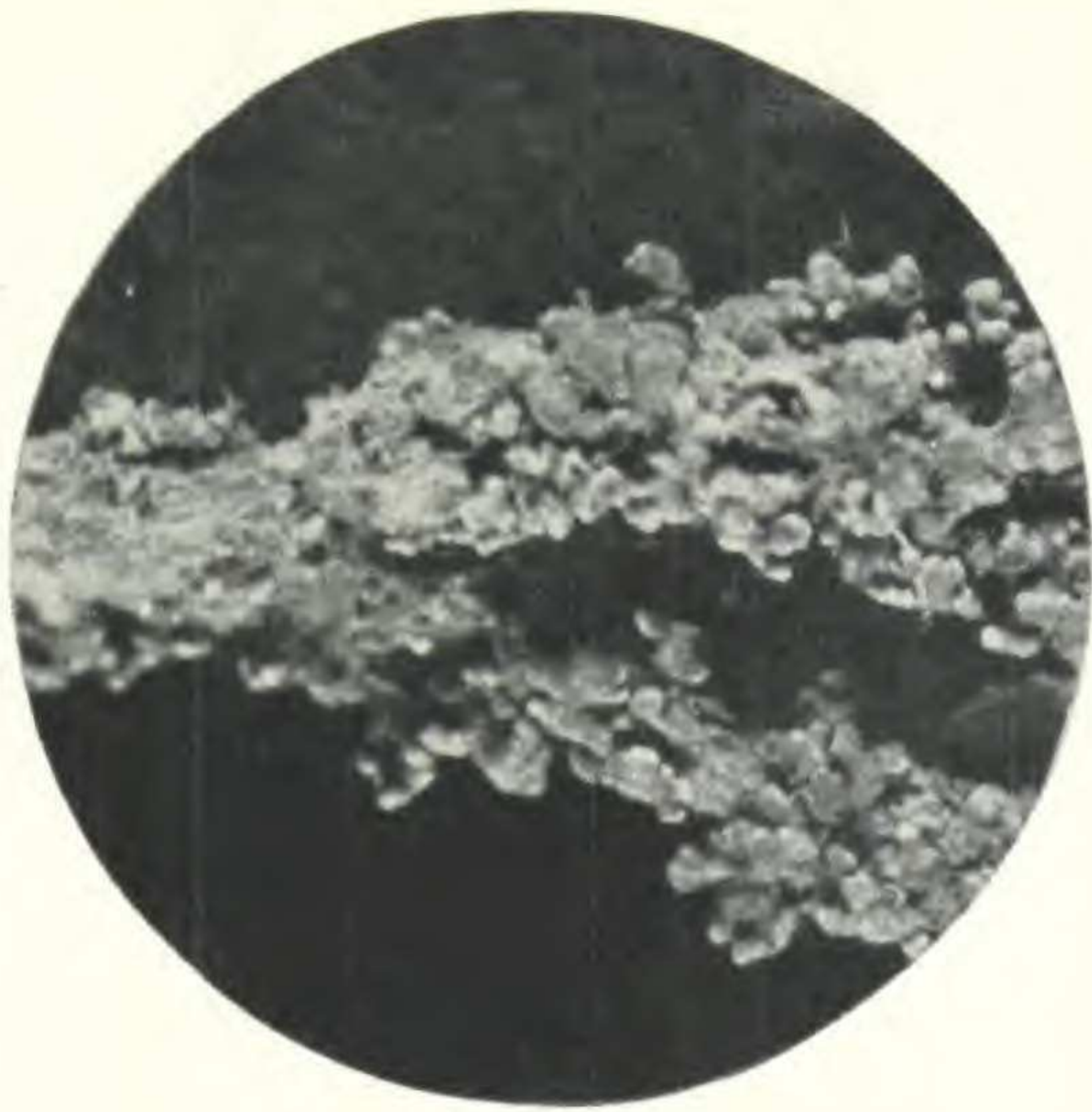
PLATE 66

Cephalodia of *Stereocaulon* illustrating their varied gross morphology (\times approx. 10 diameters).

Figs. 1 and 2. Podetial segments dissected from a species belonging to the group with spherical cephalodia. Fig. 1 shows a vertical view of three adjacent spherical cephalodia; fig. 2, a lateral view of a single cephalodium.

Figs. 3 and 4. Podetial segments dissected from a species belonging to the group with botryose cephalodia. Fig. 3 is a vertical, and fig. 4 a lateral view of cephalodia borne on them.

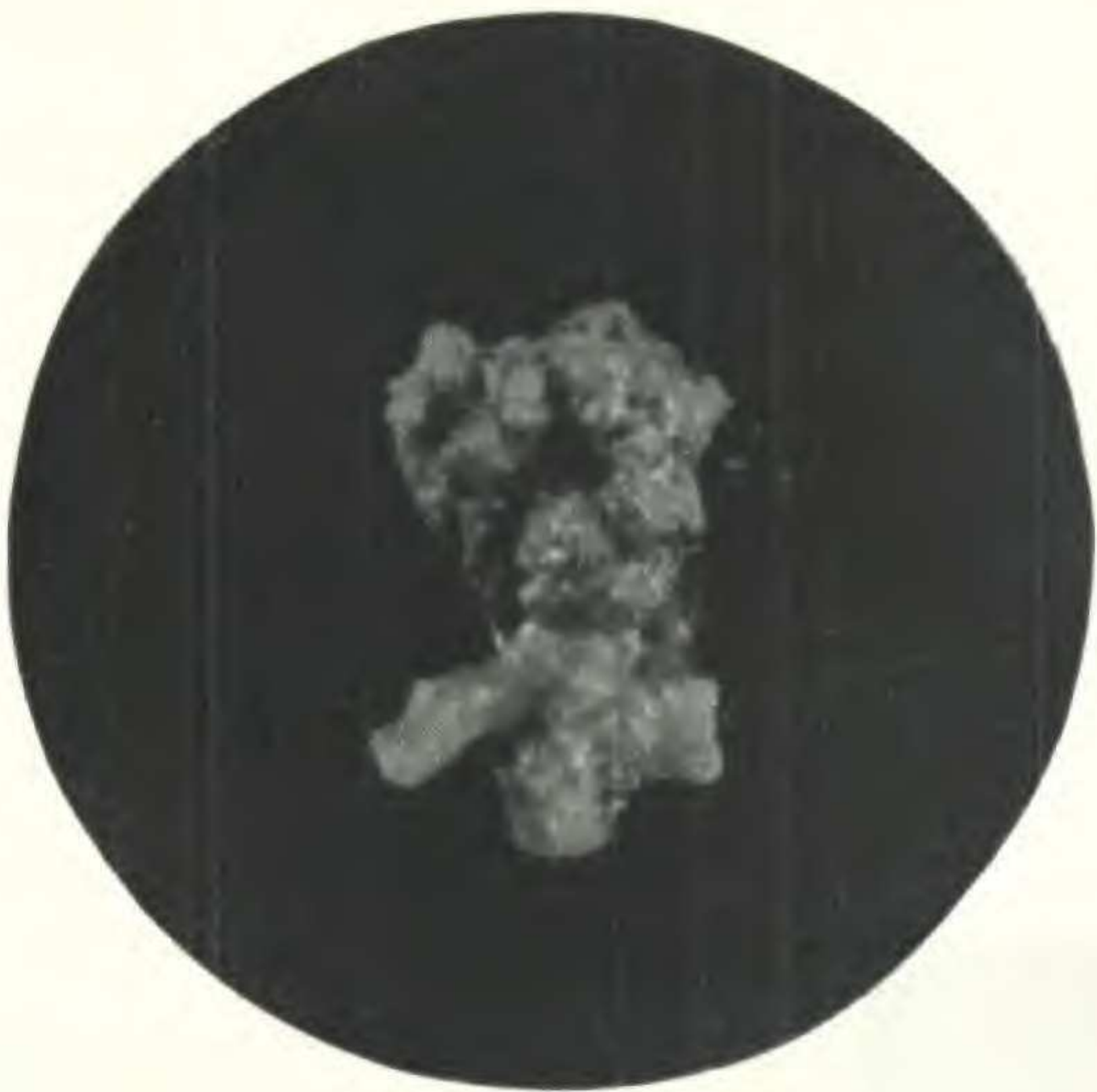
Figs. 5 and 6. These figures illustrate two podetial segments dissected from species belonging to the group with scrobiculate cephalodia. In both cases the cephalodia are seen in lateral view.



1



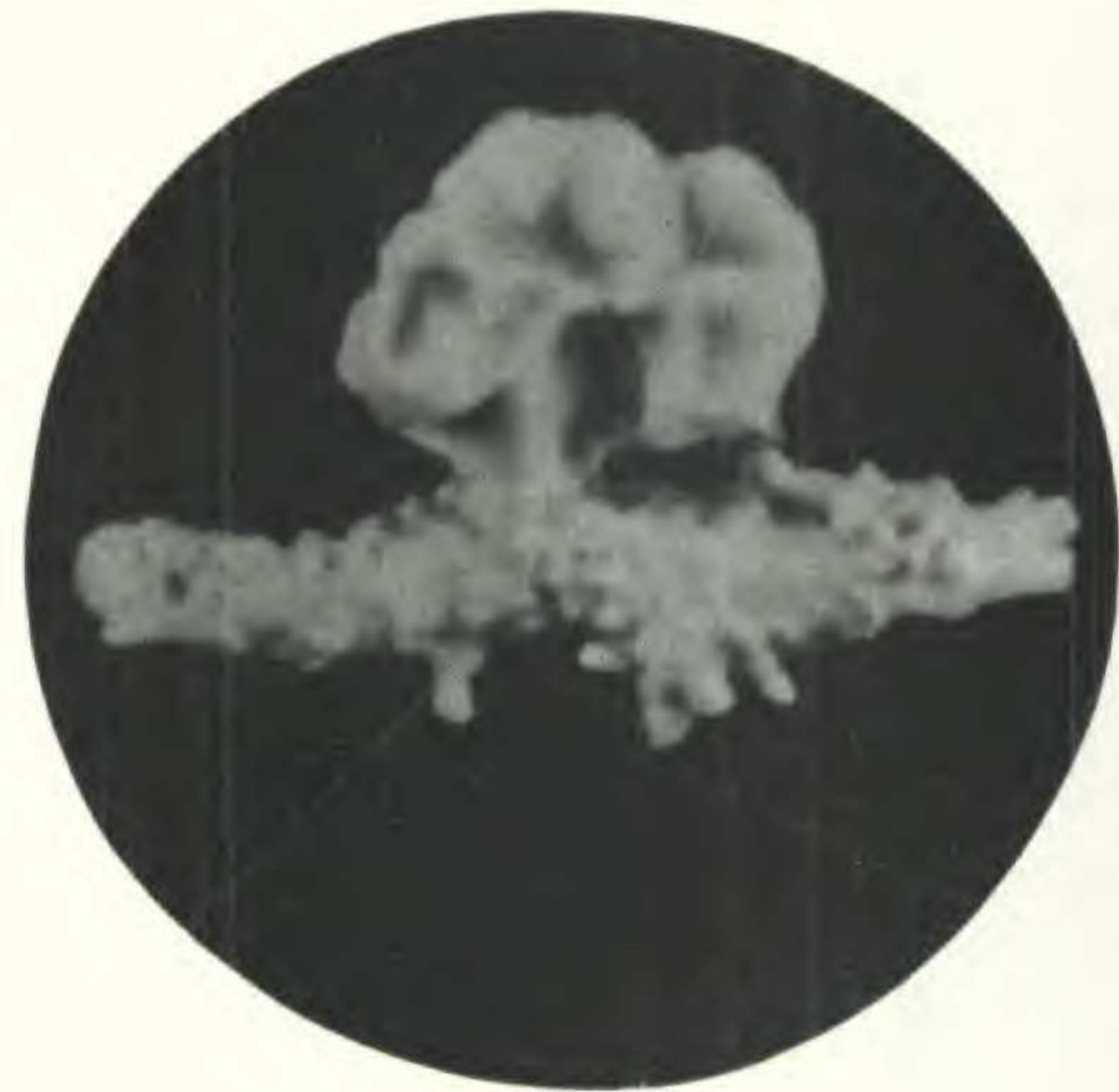
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6

JOHNSON—CEPHALODIA OF STEREOCAULON

EXPLANATION OF PLATE

PLATE 67

Photomicrographs illustrating the origin and development of cephalodia. (Magnifications approximately as follows: fig. 15, $\times 35$; figs. 4, 7, and 10, $\times 60$; figs. 1 and 6, $\times 175$; figs. 2-3, 5, 8-9, 11-14, $\times 270$ diameters.)

Figs. 1-8. Representative stages in the development of spherical cephalodia. (All photographs are of cephalodia taken from the same collection of one species.)

Fig. 1. A very early stage in the development of a cephalodium.

Fig. 2. A stage slightly later in development than fig. 1.

Fig. 3. A stage somewhat similar to fig. 2, but showing further growth and differentiation by the fungal hyphae.

Fig. 4. Vertical section through the median plane of a relatively young cephalodium.

Fig. 5. The algal masses and associated fungal hyphae.

Fig. 6. Cross-section through the upper part of a cephalodium.

Fig. 7. Vertical section of a mature cephalodium.

Fig. 8. Enlargement of the cephalodial wall, showing the peripheral orientation of the hyphae of which it is composed.

Figs. 9-15. Representative stages in the development of botryose cephalodia. (All photographs are of cephalodia taken from the same collection of one species.)

Fig. 9. A young cephalodium.

Fig. 10. The algae are separated into individual cells.

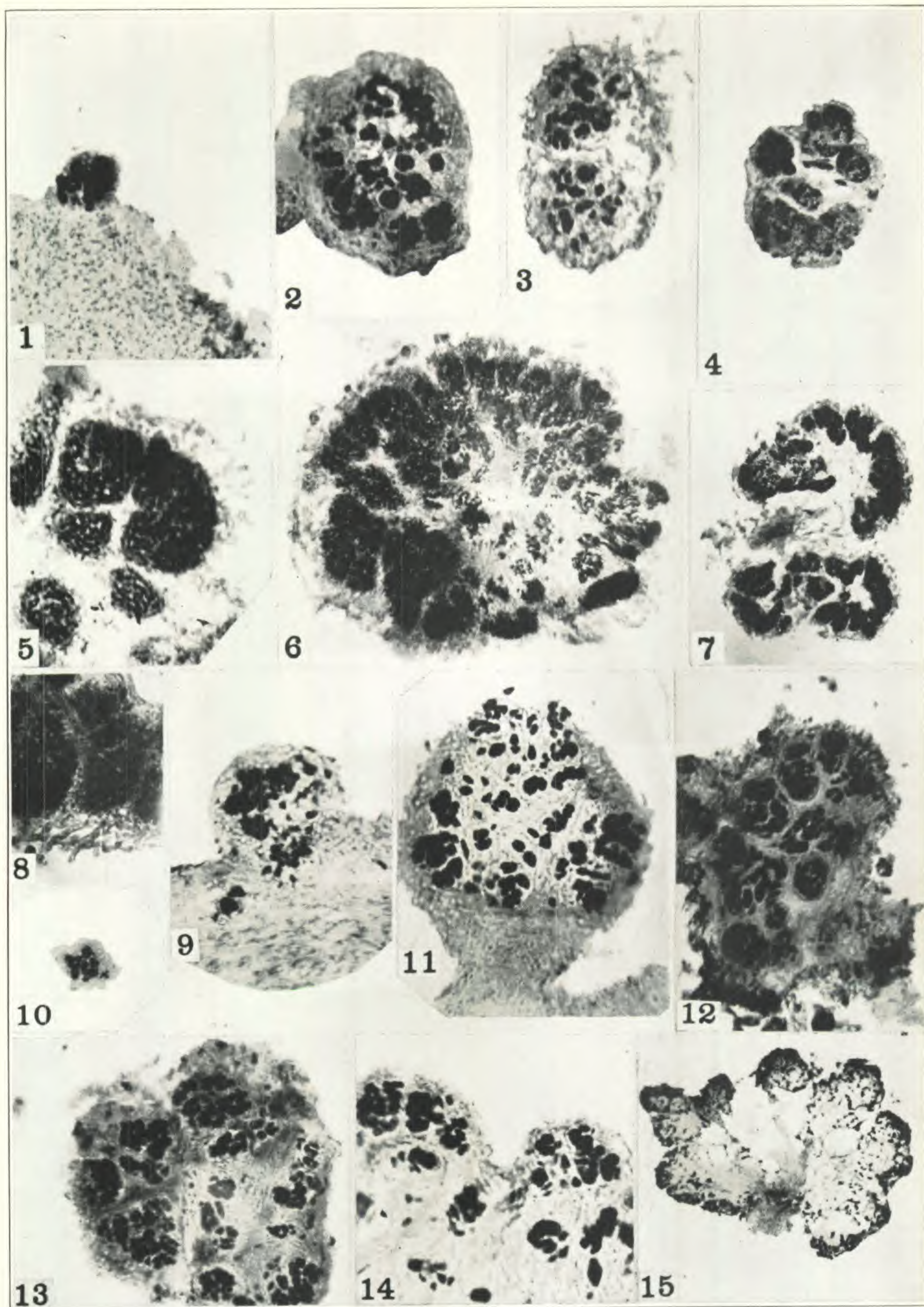
Fig. 11. Early stage in the disappearance of the gelatinous sheath shown in fig. 12.

Fig. 12. Section through a cephalodium showing the "capsular" gelatinous sheath and associated fungal hyphae.

Fig. 13. Hyphal plates give a chambered effect to the cephalodium.

Fig. 14. Enlargement of the cephalodial wall.

Fig. 15. A relatively mature cephalodium seen in vertical section through the median plane.



JOHNSON—CEPHALODIA OF STEREOCAULON

EXPLANATION OF PLATE

PLATE 68

Photomicrographs illustrating the origin and development of cephalodia. (Magnifications approximately as follows: figs. 4, 5, and 11, $\times 65$; fig. 7, $\times 260$; the rest, $\times 285$ diameters.)

Figs. 1-13. Representative stages in the development of serobiculate cephalodia. (Figs. 1-3, 6, 8, 10, and 13 are from the same collection of one species; the rest are from a single collection of another species.)

Fig. 1. Small algal cells surrounded by hyphae from the podetium.

Fig. 2. Young cephalodium developing on the wall of an older cephalodium.

Fig. 3. Young cephalodium.

Fig. 4. A relatively young cephalodium.

Fig. 5. Same as fig. 4, but at a later stage. Note especially the connection of the hyphae of the conducting core of the cephalodium with the central cylinder of the podetium.

Fig. 6. Algae from a young cephalodium.

Fig. 7. Enlargement of a sector of fig. 5, showing in detail the connection of the cephalodium with the central cylinder of the podetium.

Fig. 8. A cross-section of the cephalodial wall.

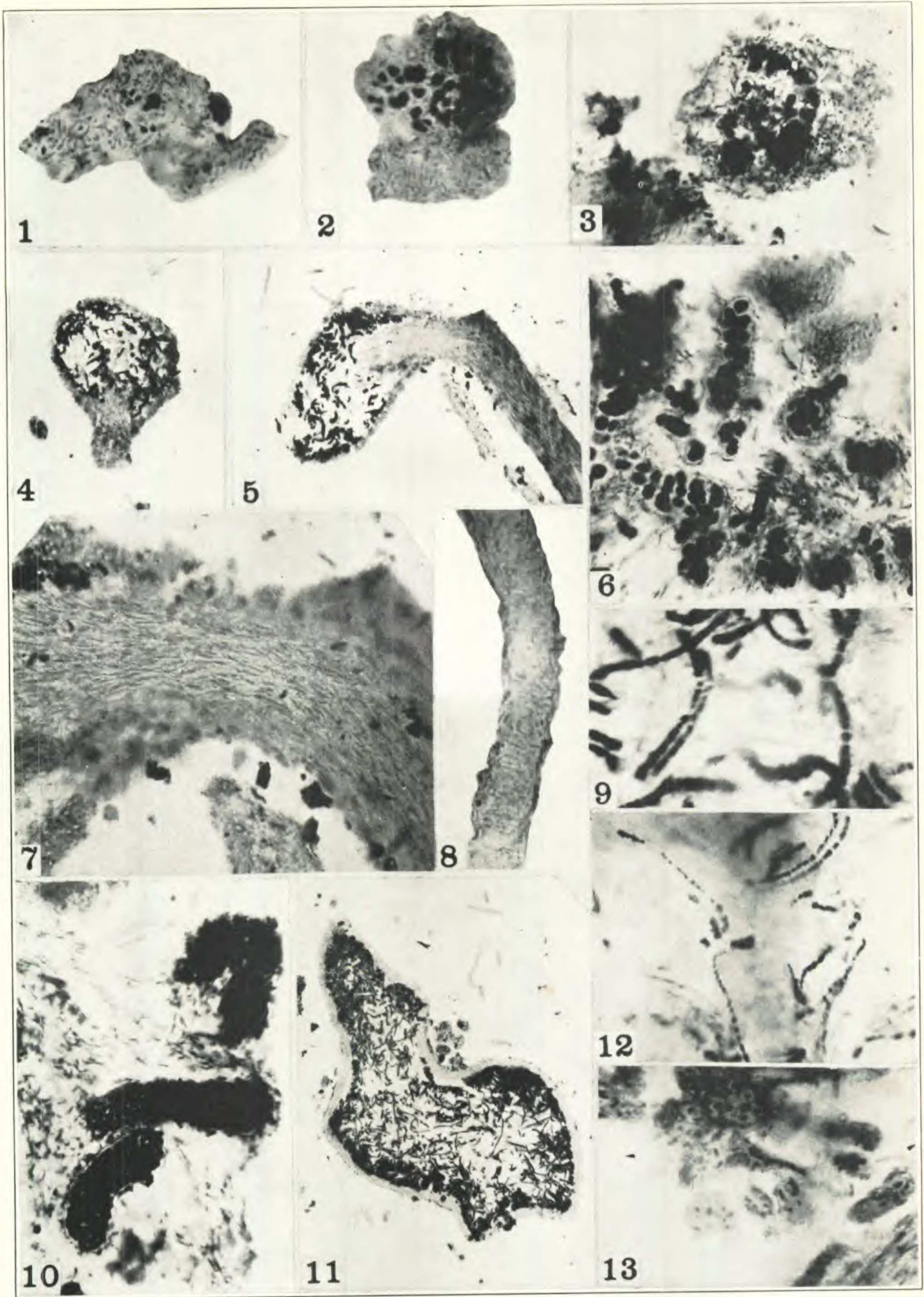
Fig. 9. Stages in the deterioration of the algae, found in older cephalodia.

Fig. 10. Algae from a relatively early stage in cephalodial development. Note the capsular structure of the algal clusters.

Fig. 11. Cross-section of a mature cephalodium.

Fig. 12. An advanced stage in the destruction of the algae in the cephalodium.

Fig. 13. Similar to fig. 12. Contrast with fig. 6, which shows the normal appearance of this species of algae.



JOHNSON—CEPHALODIA OF STEREOCAULON

NEW VARIETIES AND FORMS FROM MISSOURI

ERNEST J. PALMER

Collector and Research Assistant, Arnold Arboretum of Harvard University

AND JULIAN A. STEYERMARK

Assistant Curator of Herbarium, Field Museum of Natural History, Chicago

Taxodium distichum f. **confusum**, f. nov., ramulis arcuato-
adscendentibus; foliis brevioribus et plus adpressis quam
forma typica.

Occasionally found with the typical form, usually in open or
sunny situations.

In this form of the bald cypress the tips of the branches curve
upwards, which gives a bushy or fastigate appearance to the
tree. The leaves are shorter, crowded, and more appressed to
the branches than in the typical form, producing a somewhat
spruce-like effect. Branches and leaves of normal type are
sometimes found on the lower part of the tree.

This form should not be confused with *Taxodium ascendens*
Brong. (*T. distichum* var. *imbricatum* Groom), which it some-
what resembles in extreme forms but from which it differs in
the usually less subulate leaves and in the smoother bark.
Taxodium ascendens is not found so far inland.

MISSOURI: Markham Springs, 3 mi. w. of Williamsville, Wayne Co., June 28,
1936, *J. A. Steyermark 11261* (MBG type),¹ *11170* (MBG paratype). ILLINOIS:
Shawneetown, Gallatin Co., June 14, 1919, *E. J. Palmer 15482*, and May 12, 1923,
22589; Metropolis, Massac Co., Sept. 16, 1923, *E. J. Palmer 23752*; McClure, Alex-
ander Co., Sept. 29, 1919, *E. J. Palmer 16625*. ARKANSAS: Fulton, Hempstead Co.,
June 10, 1909, *B. F. Bush 5813*. Isotype and other specimens, A.A.

Salix sericea f. **glabra**, f. nov., foliis maturis glabris subtus.

Low ground and swampy meadows along streams, north-
eastern Ozark region and probably occasionally elsewhere with
the typical form.

¹In the citation of specimens the following abbreviations have been used:
A.A.—Arnold Arboretum Herbarium; G.—Gray Herbarium; MBG.—Missouri Bot-
anical Garden Herbarium.

This form of the silky willow differs from the normal type in having the under-surface of the mature leaves glabrous. Specimens from other regions have been seen in which the young leaves on new growth are silky while those on the older branches are glabrous as in this form. In some parts of the Ozark region the glabrous form is the only one found.

MISSOURI: along north prong (Hutchins Creek) of Meramec River, between Stone Hill and Indian Trail State Park, Dent Co., Aug. 4, 1936, *J. A. Steyermark 12918* (MBG type); along Brushy Creek, 1 mi. north of Moses Store, Reynolds Co., Aug. 13, 1936, *J. A. Steyermark 12918* (MBG paratype).

***Salix cordata* f. *mollis*, f. nov.** A typo differt foliis pubescentibus praesertim costa media subtus, petiolis ramulisque pubescentibus.

From the ordinary *S. cordata* Muhl. this form differs in the more pubescent under-surface of the leaves, especially along the midrib, and in the pubescent petioles and branchlets.

Swampy meadows and wet open ground along small streams.

MISSOURI: along spring branch of Twin Springs, between Stone Hill and Indian Trail State Park, Dent Co., Aug. 4, 1936, *J. A. Steyermark 12491* (MBG type); along Moline Creek, 7 mi. from St. Louis, April 14 and Sept. 2, 1895, *N. M. Glatfelter 25*; along Turkey Creek, near Joplin, Jasper Co., May 20, 1909, *E. J. Palmer 2043*, and July 18, 1920, *18415*; Oasis, Taney Co., June 2, 1931, *E. J. Palmer 39492*. All specimens except type and paratype in A.A.

***Salix cordata* f. *subintegra*, f. nov., foliis subintegrifolia.**

This odd form differs from normal *S. cordata* in its subentire instead of sharply serrulate leaves.

Wet rocky banks and swampy open ground.

MISSOURI: shore of lake at Yancy Mills Spring, Phelps Co., Nov. 28, 1936, *J. A. Steyermark 20910* (MBG type)

***Carya Buckleyi* var. *arkansana* f. *glabra*, f. nov., foliis glabris; ramulis annotinis glabris vel fere glabris.**

Occasionally found with the common pubescent forms in dry rocky woods, especially on cherty ridges or hillsides.

In typical *C. Buckleyi* and in the varieties *arkansana* and *villosa* the under-surfaces of the leaves and the young branchlets are thickly covered with tawny pubescence mixed with small, scurfy, silvery scales, the pubescence persisting at least along